Pliocene frogs from Langebaanweg, Western Cape Province, South Africa

D. Eduard van Dijk*

The Varswater Formation at Langebaanweg, Western Cape Province, South Africa, is known particularly for its Late Miocene–Early Pliocene mammalian and abundant avian fossils. Amphibian bones from the site are, like the avian bones, notable for their variety, surpassed in numbers of families and genera by no site in Africa and few sites in the world. The bones were transported by a river system from a variety of habitats and include those of swimmers, hoppers, leapers, burrowers and probably also climbers and torrent-associated climbers/swimmers. The fossil evidence indicates the presence of at least four anuran families and possibly as many as seven genera in six families.

Rich[1] in 1980 wrote: 'Langebaanweg is by far the richest pre-Pleistocene avian site yet discovered.' Amphibian bones from the same site were known to be numerous as early as 1972[2] but were not mentioned in a 1976 overview.[3] Two decades later, a review of southern African anuran fossil sites[4] drew attention to the Langebaanweg site, and an examination of sieved material that had been sorted as anuran at the South African Museum in Cape Town showed that various taxa were present. A poster illustrating this variety was prepared in September 1998, when a laboratory and museum were opened at the Langebaanweg site. An updated version of this material may be viewed at http://www.sun.ac.za/zoology.

The anuran bones at Langebaanweg are almost invariably isolated elements. Fortunately, the sacral bones of southern African anurans may be diagnostic at subordinal, superfamily, family or generic level and are robust enough for many to survive transport without losing their important characteristics. Two types of sacral configurations can be distinguished in the Langebaanweg fossil fauna: one in which the sacrum is an isolated bone, the other where there is fusion with the urostyle (consisting of united post-sacral vertebral elements). A fused sacrum and urostyle occurs in two extant African anuran families, the Pipidae (suborder Mesobatrachia, superfamily Pipoidea) and the Brevicipitidae (suborder Neobatrachia, superfamily Ranoidea). Both families are present as fossils at Langebaanweg.

In the Pipidae (Fig. 1a), the transverse processes (diapophyses) are much expanded, with parallel lateral edges (rarely intact in fossils), and the paired facets (prezygapophyses), which articulate with the presacral vertebrae, have longitudinal grooves. In the Brevicipitidae (Fig. 1b), the diapophyses are less expanded and have curved lateral edges, and the prezygapophyses are flat. Other bones at Langebaanweg confirm the presence of a pipid frog similar to the aquatic genus *Xenopus*, and a brevicipitid frog similar to the borrowing genus *Breviceps*.

The other sacra (those not fused to urostyles) at Langebaanweg can be divided into two groups on the basis of the articulation of the sacrum with the centrum of the eighth vertebra (presacral): in the one group (suborder Neobatrachia, superfamily Hyloidea), the sacrum has a socket (procoelous condition, similar to that of the other vertebrae), in the other (suborder Neobatrachia, superfamily Ranoidea) the sacrum has a boss (diplasiocoelous condition, in which the other vertebrae are procoelous, except for the amphicoelous presacral). The procoelous sacra (Fig. 1c) are mainly or entirely those of Bufonidae (toads) and have somewhat expanded diapophyses associated with walking and hopping locomotion.[5,6] The diplasiocoelous sacra (Figs 1d and 1e) are ranoid, with more or less cylindrical diapophyses usually associated with leaping.[5,6] There is much variation, however, and at least two genera are represented — one robust sacrum (Fig. 1e) falls outside the variation of any extant South African (and probably sub-Saharan also) genus of the Ranidae, Hyperoliidae and Rhacophoridae. Two ranid genera (family Ranidae) would mean that there are, on the basis of sacra only, at least five genera in all. The worldwide review of fossil Salientia of Sanchez[8] includes more than 1200 sites known in 1998, and fewer than 2% of these are Pliocene or older and have five or more genera.

The bones of frogs of the family Hyperoliidae, which are mainly climber/leapers, are difficult to distinguish from those of the more slender of the Ranidae. However, several bones at Langebaanweg (comprising femur, humerus, ilium fragment, scapula, and sacrum) indicate either a third, gracile ranid genus or, more likely, a hyperoliid (compare Figs 2e and 2f). A very slender, nearly straight femur with a distinct, but short, posterior proximal ridge is probably hyperoliid. The femora of Pipidae, Bufonidae, Brevicipitidae and most Ranidae have distinct curvature; a ridge is rare in ranids, except the genera of very small size. Bones of frogs of the only genus of the hyloidean family Heleophrynidae in southern Africa are mostly similar to those of the Bufonidae. However, a distinctive humerus has, proximally, a groove and complex ridges seen only in the genus *Heleophryne* among African frogs studied (Fig. 2b). The anterior vertebrae are bones with good preservation potential which, if found, could provide definite proof of the presence of the Hyperoliidae and/or the Heleophrynidae.

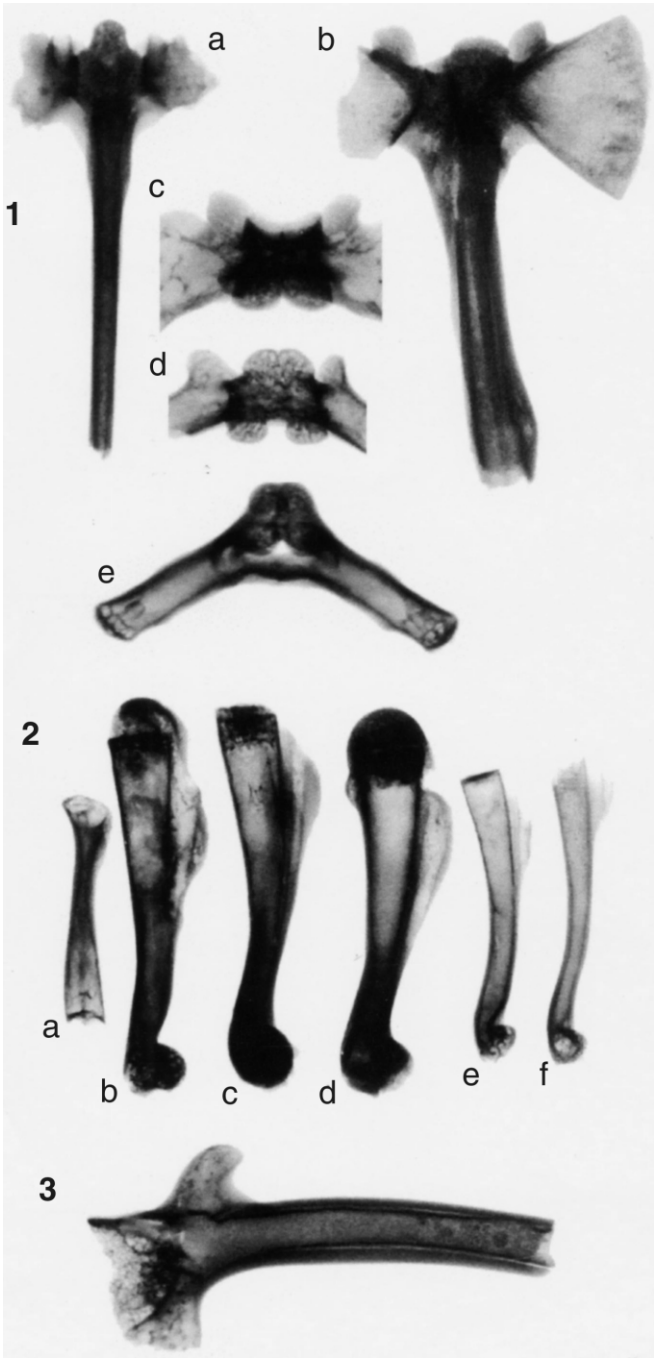
In both Hyperoliidae and Heleophrynidae the cotyles for articulation with the cranium are well separated, whereas they are close in Pipidae, Bufonidae, Brevicipitidae and most ranoids.† In Heleophrynidae, the first two vertebrae are fused, a condition normal only in brevicipitids, with close cotyles, and Hemisidae, with a highly characteristic dorsal ridge. In Hyperoliidae, the neural ridge of the first vertebra usually articulates distinctively with that of the second.

An ilium, of which there are several specimens, unlike that of any extant southern African anuran observed (Fig. 3), is characterized by a strong dorsal process at the base of the shaft, but without the crest (ala), which is associated with a strong dorsal process in ranids.

There are thus at least four anuran families at Langebaanweg: Pipidae, Bufonidae, Brevicipitidae and Ranidae. There are probably two more families represented, Hyperoliidae and Heleophrynidae. Taking the reasonable view that the ilium with the strong basal process is bufonid or brevicipitid, there are probably six families present, with one additional, ranoid genus, giving a total of seven genera in six families. With more specimens likely to be revealed in continuing research, there are only three com-

*Department of Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa.
E-mail: eddie@vandijks.com

†The degree of proximity of atlantal cotyles has proved to be a useful criterion at about subfamilial level.[8] However, when *Heleophryne* was included in an analysis, it was placed in a group with narrowly spaced cotyles (ref. 9, p. 54), although examination of the cotyles of all *Heleophryne* species indicates that they would be more appropriately placed in the widely spaced category illustrated on the same page.



Figs 1–3. X-ray images of fossil anuran bones from Langebaanweg. **1**, Sacra (a, pipid; b, brevicipitid; c, procoelan (bufonid?); d and e, ranoid). **2**, Humeri [a, pipid; b, heleophrynid; c, bufonid; d, brevicipitid; e, gracile ranid; f, hyperoliid(?)]. **3**, Ilium with strong basal process. All images were taken with X-rays (25 kV, 7 mA) on Fujicolor ASA 100 film, with standard colour processing.

parable Pliocene or older sites in the world; one in Slovakia with eight genera in six families; one in Poland with seven genera in six families; and one in Florida, U.S.A., with seven genera in five families (sites 489, 864 and 1052 in ref. 7).

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Dates from Sterkfontein indicate greater age for hominids

The discoveries made continually over the past half-century in the limestone caves at Sterkfontein, northwest of Johannesburg, give good reason to believe this to be the richest hominid fossil site in the world. In spite of decades of close study, however, it has been impossible to date the fossils directly. Instead, specimen ages have been inferred by comparison with fossils accurately dated elsewhere — such as animal remains and artifacts enveloped in volcanic sediments of known radiometric age in East Africa — and in relation to how the cave system records reversals in the Earth's magnetic field.

Researchers at the University of the Witwatersrand and in the United States have now published the first results of a radiometric method that purports to give absolute dates for Sterkfontein.[1] The method, which has been tested on cave deposits in Kentucky and Virginia, depends on measuring the ratio of cosmogenic ^{26}Al and ^{10}Be in quartz particles adjacent to the fossils of interest. Knowing the respective rates of radioactive decay, and on the assumption that the indicator isotopes of aluminium and beryllium did not accumulate after burial (which means in practice that the samples must be relatively deeply buried and thus shielded from cosmic rays), it is possible to derive the time since burial.

Five burial samples were so tested; three adjacent to the nearly complete Little Foot skeleton (designated StW 573), and two from Jacovec Cavern, some 50 metres distant, where hominid and faunal remains, also described in the *Science* paper, have been newly discovered.

On this basis, Granger determined the burial age of the skeleton to be 4.17 ± 0.14 million years (Myr), corresponding to the Lower Pliocene. This is substantially older than the 3.3 Myr first proposed by Clarke *et al.*[2] and even more so than the less than 3 Myr argued last year by Berger *et al.*[3] At 4 million years, StW 573 and the Jacovec specimens are of a similar age to *Australopithecus anamensis* from East Africa, yet, according to Clarke, Little Foot does not resemble *A. anamensis* in crucial respects. Thus, there may have been more diversity among the australopithecines in the Lower Pliocene than has been supposed. Whether this is so may emerge when more hard data on these fossils are published.

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